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Chrysophyte cysts from lake sediments reveal the submillennial winter/spring climate variability in the northwestern Mediterranean region throughout the Holocene

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Abstract In the last decade, much effort was dedicated to the reconstruction of past climate at high temporal resolution. Here, we show the suitability of chrysophyte cysts from lake sediments for revealing continental climate variability when used in sensitive sites, such as those in high mountains. We demonstrate that altitude is a main factor influencing the present distribution of chrysophytes and develop a transfer function to evaluate the local “altitude anomaly” on a lake site throughout time. Based on our knowledge of chrysophyte ecology, the altitude anomalies are interpreted as winter/spring climate signatures. The method was applied to a Holocene record from a lake in the Pyrenees showing submillennial climatic variability in this northwestern Mediterranean zone. A warming trend was present from the early Holocene to 4 kyear BP. Comparison with pollen-based reconstructions of summer temperatures denoted a contrasting decrease in continentality between the two parts of the Holocene. Oscillations of 1 cycle per ca. 2,000 years appeared throughout the record. The warmest Holocene winters were recorded during the Medieval Warm Period at ca. AD 900 and 450 and the Roman Warm Period (2.7–2.4 kyear BP). Winters in the period AD 1,050–1,175 were inferred to be as cold as in the Little Ice Age. The period between 3 and 7 kyear BP showed lower intensity in the fluctuations than in early and late Holocene. The cold event, 8,200 years ago, appeared embedded in a

warm fluctuation. Another cold fluctuation was recorded around 9 kyear BP, which is in agreement with Irish and Greenland records.

1 Introduction

Compared with marine records, continental climate reconstructions may show more geographical variability due to local and regional peculiarities; the use of a broad collection of proxies may help in disentangling the geographical complexity. Each proxy has its advantages and shortcomings; properties such as sensitivity, reproducibility, local availability and continuity through time differ among them (Mann 2002). When trying to reconstruct Holocene climate fluctuations the difficulties increase (Broecker 2001). As the mean annual temperature fluctuations were low, there are very few sensitive proxies and some do not extend back sufficiently in time. And, in addition, human activity during the late Holocene conditioned some proxies and disturbed many sites. Therefore, understanding climate variability throughout the Holocene is a difficult task of assembling many diverse pieces of work at many sites. However, this period can provide important clues as to how climate may change in our immediate future.

The accuracy of the temperature estimates based on floral and faunal remains from lake and bog sediments is in the range of ca. $\pm 1^\circ\text{C}$ (Lotter et al. 2000; Rosén et al. 2000; Bigler and Hall 2002; Bloom et al. 2003; Heiri et al. 2003), which may not be sufficient for the Holocene fluctuations (Broecker 2001). However, this limitation might be less severe than it apparently seems to be. Mean annual temperature is sufficient to summarise large climatic variations. The fluctuations are so large that any biological proxy that is minimally related to temperature will indicate warm and cold periods. However, when entering the range of 1° fluctuations,

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mean annual temperature has a limited meaning in an ecological context. The impact on biological sensors depends on how the fluctuations are seasonally distributed and whether they affect a key activity period. Therefore, given the large number of proxies and recording sites on the continents, there is some chance that some records track climatic components with the accuracy required for the Holocene fluctuations.

Alpine palaeolimnology is increasingly becoming more relevant in the present global change context, because of the sensitivity shown by mountain ecosystem to atmospheric forcing (Psenner and Schmidt 1992; Wolfe et al. 2001; Battarbee et al. 2002), and the possibility to use the altitudinal climatic gradient for calibrating the proxies (Vyverman and Sabbe 1995) in a space for time approach. In addition, the records in alpine lakes are usually uninterrupted since the lake formation; and this property is particularly useful in semi-arid regions where it can be difficult to find sites with continuous records throughout long time periods (Olago 2001). In this paper, we present the case of chrysophyte cysts assemblages in mountain lakes as a palaeoclimatic tool. We also show how the assemblages of cyst morphotypes change with altitude and, as a consequence, how they can be used to reconstruct local “altitude anomalies” as surrogates for climate fluctuations.

Chrysophytes (classes Chrysophyceae and Synurophyceae) are a diverse group of primarily freshwater algae with over 1,000 known species. They are common and often dominate phytoplankton assemblages of temperate and cold oligotrophic lakes (Eloranta 1995; Sandgren 1988; Siver and Hamer 1989; Felip et al. 1999), and possess two key features for palaeoenvironmental reconstruction. They produce resting siliceous cysts (stomatocysts) (Duff et al. 1995; Wilkinson et al. 2001), and there is a correlation between the number of live cells and the number of cysts produced (Sandgren 1988). Therefore, the cysts preserved in the sediments provide a good record of the dynamics of the algal populations in the water column over a period of time (Zeeb et al. 1990, 1994; Kamenik et al. 2001; Betts-Piper et al. 2004).

Climate fluctuations can affect the abundance and composition of chrysophytes by influencing water temperature (Livingstone and Lotter 1998), modifying resource availability (light and nutrients), environmental conditions (pH, alkalinity and redox) or the physical system (extent of ice cover, duration of summer stratification and mixing patterns) (Siver 1995; Siver and Hamer 1992; Smol and Cumming 2000). Given the number of factors and the complexity of the processes involved, a mechanistic model relating a climatic parameter (e.g. air temperature) to chrysophyte cyst composition becomes intractable at present.

In our study, we looked for a statistical model tailored to the conditions of its application in a Pyrenean site (NE Spain). Therefore, we first studied the cyst distributions in modern surface sediment samples from high mountain lakes in the Pyrenees. The lakes studied covered a broad range of altitude, size, and bedrock and

vegetation types. Altitude can be considered a surrogate for climate, because, above 1,600 m a.s.l. where the lakes are situated, there are no significant thermal inversions, and temperature changes according to altitude by a proportionality factor (lapse rate) characteristic of each month (Agustí-Panareda and Thompson 2002). With a series of multivariate analyses we tested whether altitude is a significant factor in determining chrysophyte cyst distributions, and to what extent it is independent from other factors, such as bedrock, which determines the major chemical features of water in the Pyrenean lakes, particularly alkalinity (Catalan et al. 1993). Interestingly, altitude appeared to be orthogonal to the axis of variability defined by different bedrocks. In other words, a significant part of the variability in the distribution of chrysophyte cysts was related to altitude and was independent of the chemical characteristics of the water. Therefore, in the course of the history of a lake, in which the range of the water chemical fluctuations is certainly narrower than in the set of lakes surveyed, we could expect changes in chrysophyte cysts to be reliable indicators of changes in climate.

A second step was to develop a transfer function to evaluate, from the cyst sediment record, the “altitude anomalies” experienced by a lake throughout time. To minimise any noisy influence on the transfer function provided by water chemistry gradients or other features related to the bedrock nature of the catchment, we restricted the calibration set to lakes with dominant granodioritic substrate, which was the catchment bedrock of the lake where we planned to apply the method.

In addition to the calibration of the model, in this paper, we present an application to a lake sediment record covering the Holocene in the Pyrenees. We discuss the climatic interpretation of the “altitude anomalies” reconstructed and carry out a comparison with documentary and high-resolution proxy records from the Northern Hemisphere.

2 Materials and methods

2.1 Data set

The chrysophyte cyst data set consisted of 114 samples from 105 lakes in the Central and Eastern Pyrenees (NE Spain) and was developed in the course of four surveys (1987, 1995, 1996 and 1998), during the summer season (Fig. 1). Surface sediment samples were collected by diving between 2 and 6 m deep in the 1987 and 1995 surveys, and by using a gravity corer in the deepest part of the lake in the 1996 and 1998 surveys. The upper 0.5 cm of sediment was analysed.

The lakes were chosen from among the ca. 500 of this area, to provide a broad range of altitude (1,615–2,954 m a.s.l.), size (0.7–45.4 ha), depth (1–80 m), bedrock (major chemistry) and vegetation types (trophic state) (Fig. 2). The parameter distribution for the lakes surveyed roughly reflects the distribution for the whole

Fig. 1 Map indicating the location of the lake Redon coring site and 104 high-mountain lakes sampled to study the chrysophyte cyst distributions in the Pyrenees. Lake codes follow Pla (2001), where details for each lake can be found. The dominant bedrock type is indicated

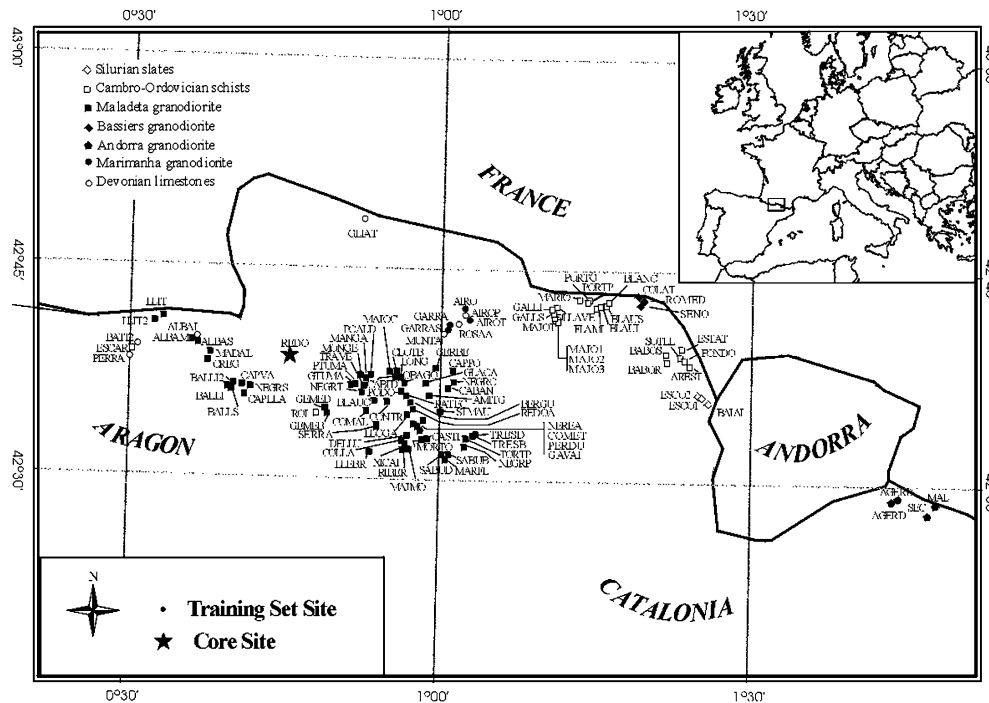
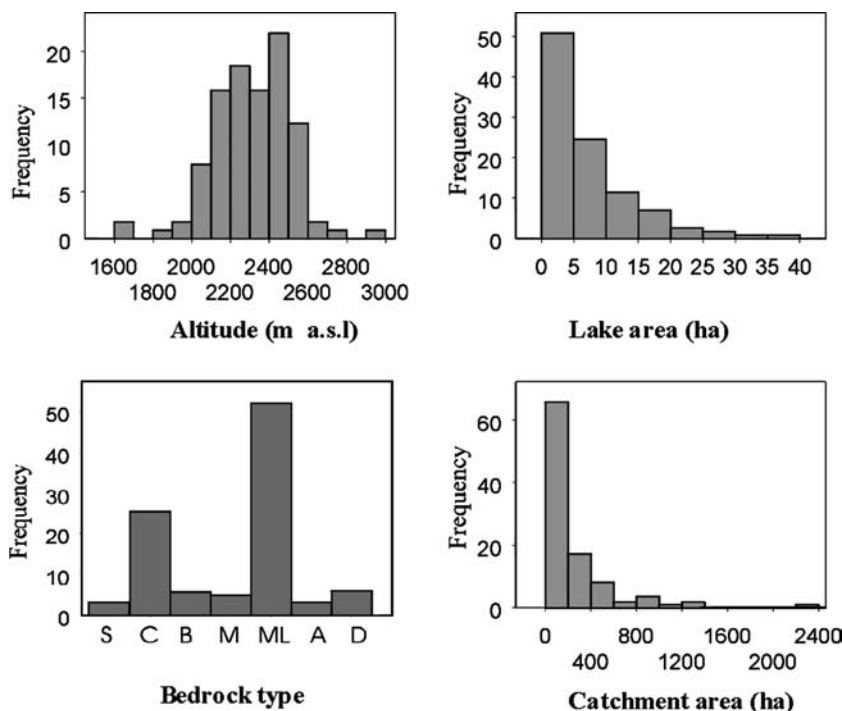


Fig. 2 Histograms showing the distribution of some lake characteristics relevant to the chrysophyte cyst distributions. Dominant bedrock types include Silurian slates (S); Cambro-Ordovician schists (C); granodiorite from Bassiers (B), Marimanha (M), Maladeta (ML), and Andorra-Montlluis (A) batholiths; and Devonian limestones (D)



set of lakes in the area. Most lakes were on granodioritic bedrock distributed over four batholiths (Maladeta, Bassiers, Andorra-Montlluis and Marimanha) that cover around 70% of the total lake catchment areas. The rest of the lakes were on Cambro-Ordovician schists and phyllites, except a few that had Silurian slates rich in sulphides and some others with Devonian limestones. Catchment vegetation was generally poorly developed. *Festuca eskia* meadows were almost

always present and constitute the dominant vegetation in 39% of the catchments. *Rhododendron ferrugineum* with some sparse pines (*Pinus uncinata*) were common in 24% of the catchments. *Pinus uncinata* forests and *Carex curvula* meadows (13%) were also present. Llebrera, the lowest lake studied, was the only one with a montane forest. Thirty percent of the lakes had 10% or more of their shoreline composed of *Sphagnum* bogs.

An environmental data matrix was developed including geographic, geomorphologic, vegetation and bedrock variables (Table 1). The degree of vegetation development was included using a rank variable (1, *Festuca* meadows; 2, *Carex* meadows; 3, *Rhododendron* bush; 4, pine forest; and 5, montane forest). The percentage of the lake shoreline covered by bogs was introduced to take into account the potential influence of those neighbour systems in the chrysophyte assemblages of the lake. It was assumed that those landscape factors would embrace any significant gradient in proximal factors (such as water chemistry, temperature, and water renewal) determining the distribution of chrysophyte assemblages. The full data matrix can be found in Pla (2001).

2.2 Chrysophyte cyst preparation and identification

All samples were treated with hydrogen peroxide (33% H₂O₂) and some drops of HCl. The resulting siliceous slurries were mounted in Naphrax (R.I. = 1.7) following Battarbee (1986). Stomatocysts were identified and described, based on surface morphological features observed using a scanning electron microscope (SEM; LEO Stereoscan 360) and assigned numbers according to the guidelines of the International Statospore Working Group (Cronberg and Sandgren 1986; Duff et al. 1995; Wilkinson et al. 2001). Cyst numbering and all cyst descriptions can be found in Pla (2001). Stomatocysts were counted using a Reichert–Jung Polyvar light microscope (LM) equipped with differential interference contrast (Nomarski), under oil immersion at 1200×. A minimum of 300 chrysophyte cysts were identified and counted along transects from each sample slide. In some cases, cysts that could be distinguished under SEM were indistinguishable using LM. These cysts were counted as a collective category (e.g. S042/49). Only the morphotypes with relative abundance >1% in at least one

sample were considered in the numerical analysis and the 210 cysts identified were reduced to 152.

2.3 Numerical methods

The relationship between environmental factors and cyst distribution was assessed by a series of canonical correspondence analyses (CCA) (Jongman et al. 1995). CCA is a direct gradient analysis technique that simultaneously represents cyst taxa, samples and environmental variables in a low multidimensional space, where axes are constrained to be linear combinations of environmental variables. In the analyses we downweighted rare species. The redundancy of environmental information was determined using a variance inflation factor (VIF) (Montgomery and Peck 1982). The VIF is related to the partial multiple correlation between a certain environmental variable and the other environmental variables in the analysis. Variables with VIF >25 were removed from the analysis because it was an indication that they had a high degree of collinearity with at least one of the other variables in the data set (ter Braak 1986). Samples with high influence (leverage >×5, Montgomery and Peck 1982) on a given environmental variable were also removed from the data set to avoid spurious relationships. Then the significance of each remaining variable was tested with Monte Carlo permutation (999 permutations, $p < 0.005$) (Birks et al. 1990). A forward selection was carried out to reduce the number of variables (Birks 1998) and partial CCAs were used to investigate the unique contribution of each forward selected variable to the variance explained by the selected environmental variables (Borcard et al. 1992). All the analyses were carried out using the CANOCO program (ter Braak 1992).

Among the several techniques available using biotic data as a tool for reconstructing past variables (ter Braak and Juggins 1993), weighted-averaging partial

Table 1 List of the environmental factors considered

Number	Variables name (acronym)	Type	Category
1	Latitude (lat)	Quantitative	Geographical
2	Longitude (long)	Quantitative	Geographical
3	Altitude (alt)	Quantitative	Geographical
4	Catchment area (catch) (ha)	Quantitative	Geomorphological
5	Lake area (area) (ha)	Quantitative	Geomorphological
6	Percentage of shoreline with bogs (bog)	Quantitative	Vegetation
7	Silurian schists (rsil)	Nominal	Bedrock
8	Cambro-Ordovician slates (rcam)	Nominal	Bedrock
9	Maladeta granodiorite (rgmal)	Nominal	Bedrock
10	Bassiers granodiorite (rgbas)	Nominal	Bedrock
11	Andorra-Montlluis granodiorite (rgand)	Nominal	Bedrock
12	Marimanha granodiorite (rgmar)	Nominal	Bedrock
13	Devonian limestones (rcal)	Nominal	Bedrock
14	<i>Festuca</i> meadows (vf)	Nominal	Vegetation
15	<i>Carex</i> meadows (vc)	Nominal	Vegetation
16	<i>Rhododendron</i> bush (vr)	Nominal	Vegetation
17	Pine forest (vp)	Nominal	Vegetation
18	Montane forest (vfo)	Nominal	Vegetation
19	Vegetation complexity (veg)	Rank	Vegetation

least squares (WA-PLS) provided the best results in terms of root mean square error of cross-validation using a leave-one-out method (RMSEP). WA assumes unimodal species responses to environmental variables and is based on a niche-space partitioning concept or, in other words, it estimates environmental optima for each species. It performs well with species-rich data with long environmental gradients but ignores residual correlation among biological data (Birks 1998). PLS uses residual correlation to improve the fit between biological data and a given environmental variable. Different data transformations were tested but none improved the results obtained using cyst percentages. Bootstrapping was used to assess error bars in the reconstruction (Birks 1995).

A modern analogue procedure was applied to the pollen record to reconstruct air temperatures of the warmest, and the coldest months. The degree of analogy between modern and past pollen assemblages was measured with a chord distance (Guiot 1990). For each fossil pollen assemblage, the four most similar modern assemblages were selected from a database including present pollen and air temperature data (Cheddadi et al. 1996).

2.4 Core sampling and dating

The coring site was Lake Redon (formerly Redó) (42° 38' 33" N and 0° 46' 13" E) located in the central Pyrenees at 2,240 m a.s.l. It has a surface area of 24 ha, a maximum depth of 73 m, and a mean depth of 32 m. Average water residence time is >4 years (Catalan 1988). The catchment area is a small granodiorite basin (155 ha); 74% is soil generally <30 cm deep and the rest is bare rock. Vegetation consists of high mountain grasslands (mainly *Festuca eskia*). Details on the physical features and chemistry can be found in Ventura et al. (2001). The lake occupies an intermediate position within the range of lakes surveyed in terms of altitude and chemistry, and thus was appropriate for the transfer function developed.

In August 1994, a sediment core (RCA94) was taken from the deepest part of the lake using a gravity corer. The total length of the core was 56 cm, and it was extruded immediately and sliced in 3-mm sections. The top 8 cm were ²¹⁰Pb dated (Appleby and Oldfield 1978); details were described in Camarero et al. (1998). Samples for AMS ¹⁴C dating were selected by performing a stratigraphically constrained cluster analysis from previous diatom analysis (Pla 1999). The results indicated eight zones with significant changes in their species assemblages, and thus nine bulk sediment samples were selected, because wood or other terrestrial vegetation remains were not available. Beta Analytica Inc. (Miami, FL, USA) processed samples. The INTCAL98 calibration procedure was followed for dates calibration (Stuiver et al. 1998). A pollen analysis was performed to check the agreement of ¹⁴C dating with the pollen

chronology previously established in the Central Pyrenees. Samples were prepared using a standard procedure (HCl, NaOH, sieving, hot HF, HCl, and Erdtman's acetolysis and dehydration; Moore et al. 1991) and mounted in silicon oil (2000 cs). Pollen was identified and counted at a magnification of 640× (1,000× for critical determinations) until a sum of at least 500 pollen grains was obtained. Loss on ignition (LOI) at 550°C was carried out as an estimation of the organic content of the sediment samples (Heiri et al. 2001).

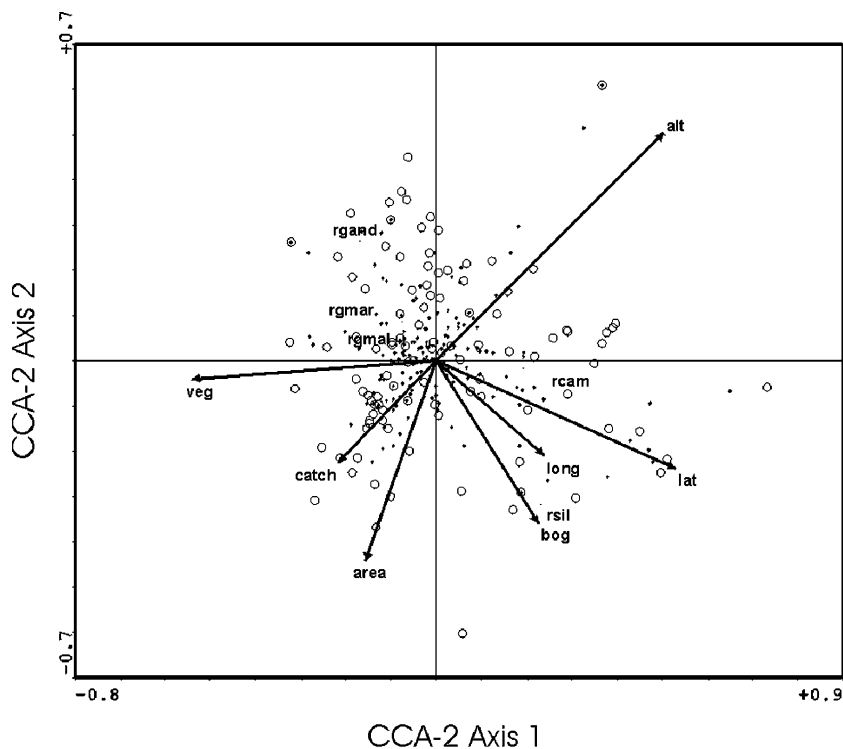
3 Results and discussion

3.1 Environmental factors and chrysophyte cyst distributions

According to the CCA results and Monte Carlo testing, all the 19 environmental variables considered (Table 1) significantly ($p < 0.05$), explained some of the variability in the distribution of cyst assemblages. To reduce the redundancy between variables a forward selection was carried out, which reduced the variables to 12 (rcam, alt, lat, bog, rgmar, rsil, cath, long, rgand, area, rgmal, and veg; ordered by variance explained). These variables explained 21.3% of the variance in the cyst data. In Fig. 3, we show the biplot defined by the two main axes, which accounted for 9.4% of the total cyst variability, being 44.2% of the variability explained by the total set of environmental variables. In the biplot, rock types determined a gradient that can be easily attributed to water chemistry (Catalan et al. 1993). The gradient ranged from acidic and very soft water in catchments with slates and schists (rsil and rcam) to neutral and better-buffered waters in most granodiorite bedrocks (rgand, rgmar and rgmal). The percentage of bogs in the shoreline of the lake followed (decreasing) the same gradient—because *Sphagnum* prefers very soft waters—as did longitude and latitude, in this case indicating a geographical pattern in rock distribution (Fig. 1). On the other hand, lake and, especially, catchment area negatively aligned with altitude, which is an obvious consequence of the impossibility of finding large catchments at the top of the mountains. Complexity of vegetation also increases as one goes down into the valleys, and is therefore negatively correlated to altitude. However, the most interesting aspect was the orthogonal position of the altitude gradient with respect to the axis defined by rock types (Fig. 3).

This result indicated that some chrysophytes respond to proximal factors related to altitude independently of how they or other chrysophytes respond to chemical changes. A further check of the independent value of altitude in explaining the cyst distribution was carried out by performing a series of partial CCAs. We introduced only one of the forward selected variables in the analysis and had the rest of the other forward selected variables as covariables in order to address the unique contribution of each variable to the variance explained

Fig. 3 The distribution of lakes, cysts and some environmental factors in the ordination plane defined by the two main axes of a canonical correspondence analysis. Quantitative environmental variables are indicated by vectors (alt, altitude; area, lake area; bog, percentage of lake shoreline with bogs; catch, catchment area; lat, latitude; long, longitude; veg, vegetation complexity), and nominal variables (catchment dominant bedrocks) are represented by their centroids (rsil, Silurian slates; rcam, Cambro-Ordovician schists; rgmal, granodiorite from Maladeta's batholith; rgmar, granodiorite from Marimanha's batholith—quoted in order of increasing alkalinity supply, which results from the rock chemical weathering). *Solid* and *open circles* indicate cysts and sites, respectively



(Birks 1998). Altitude was the variable with the highest and most significant unique contribution to the explained variance (Table 2), followed by variables indicating geographical patterns. Although some variables did not make statistically significant unique contributions, there was still a relatively large proportion of variables that contributed significantly. This fact indicated that there could be some difficulties in extracting the altitudinal (climatic) control over the chrysophytes from the data and develop a low noise altitude transfer function.

Figure 4 shows the most common cysts distributed according to their preference for lake altitude; cysts with clear preference for high altitude (S420, S041N, S397,

S202, S056B, S390 and S310) and for low altitude lakes (S231, S402, S131, S226, S135, S318, S229, S136 and S089) are evident. Clustering constrained by altitude (Grimm 1987) showed that changes in assemblages occur regularly along the altitude gradient, indicating progressive rather than step-like changes in the assemblages, a feature that positively contributed to their eventual application in developing models for quantitative reconstructions.

3.2 Altitude transfer function

The results from the previous section indicated that some environmental gradients other than altitude could generate some difficulties in developing a low noise transfer function. A relevant part of these additional gradients was related to the bedrock gradient and its geographical distribution (Fig. 3, Table 2). Therefore, to facilitate the extraction of the altitude (climate) signal, we selected only the lakes on granodioritic bedrock to develop the transfer function. The coring site and most lakes in the Pyrenees are located on this substrate (Fig. 2). As the altitude and the bedrock environmental gradients are largely orthogonal, the selection did not compromise the reliability of the transfer function, whereas it reduced the statistical noise in it. The 75 lakes used ranged in altitude from 1,615 to 2,666 m a.s.l., with mean and median values of 2,301 and 2,308 m, respectively. This altitudinal range represents a mean annual air temperature of ca. 6°C (Agustí-Panareda and Thompson 2002). Among the distinct statistical tech-

Table 2 Unique contribution of each environmental variable to the explain the chrysophyte cyst distributions

Variables	Fraction of explained variance (%)	Fraction of total variance (%)	p Value
Alt	11.6	2.5	0.001
Lat	9.8	2.1	0.001
Long	8.2	1.7	0.003
Cath	7.3	1.6	0.009
Rgand	7.0	1.5	0.009
Bog	6.7	1.4	0.006
Rgmar	6.1	1.3	0.018
Rgmal	6.0	1.3	0.014
Rsil	6.0	1.3	0.035
Rrea	5.8	1.2	0.039
Veg	5.7	1.2	0.022
Rcam	4.2	0.9	0.030

Variables acronyms as in Table 1

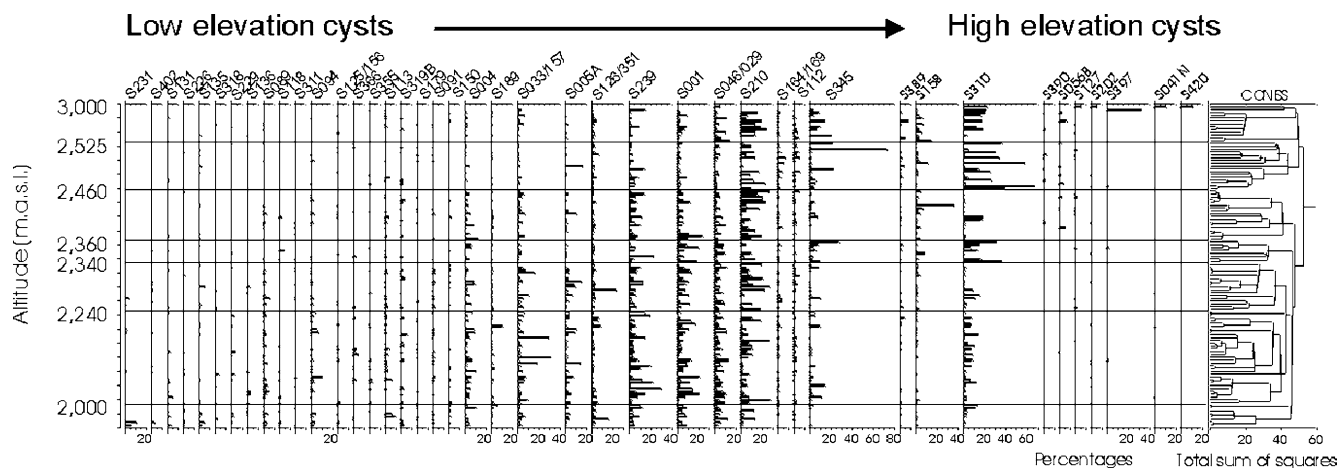


Fig. 4 Distributions of the most common cysts in the data set in relation to altitude

niques available for developing transfer functions, WA-PLS provided the best results. WA-PLS component 2 resulted in a lower root mean squared error of prediction (RMSEP) and higher jack-knifed- r^2 than classical WA (Table 3). The RMSEP for WA-PLS component 2 was 122 m, which in terms of mean annual temperature would be ca. 0.7°C. This value is within the lower range obtained employing biological remains in lakes, such as diatoms and chironomids (Lotter et al. 1997; Walker et al. 1997; Rosén et al. 2000; Larocque et al. 2001; Bigler and Hall 2002; Bloom et al. 2003; Heiri et al. 2003). A chrysophyte cyst transfer function has the advantage of presenting a lower potential interference by water chemistry changes than diatoms (e.g. diatoms are very sensitive to pH (Birks et al. 1990)) and uses a significantly larger number of taxa than training sets based on chironomids (Larocque et al. 2001).

Prediction using WA-PLS has a certain tendency to systematically overestimate low values and underestimate large values (Fig. 5a). This edge effect is inherent to the regression methods (Birks 1998). However, the independence between residuals and predicted values indicated that the transfer function

was performing satisfactorily within the experimental range (Fig. 5b).

Table 3 Summary of the altitude (m a.s.l.) transfer function statistics

	WA-classical	WA-PLS component 2
Fitting response		
RMSE (m)	117.4	74.6
r^2	0.753	0.867
Average-bias (m)	-0.793	-0.002
Maximum-bias (m)	87.855	67.773
Cross-validation response		
RMSE prediction (m)	143.6	122.0
r^2 -prediction	0.546	0.653
Prediction average-bias (m)	10.342	6.835
Prediction maximum-bias (m)	164.13	174.12

The calibration set consisted of 75 lakes and 153 taxa. Cross validation was carried out by jack-knifing

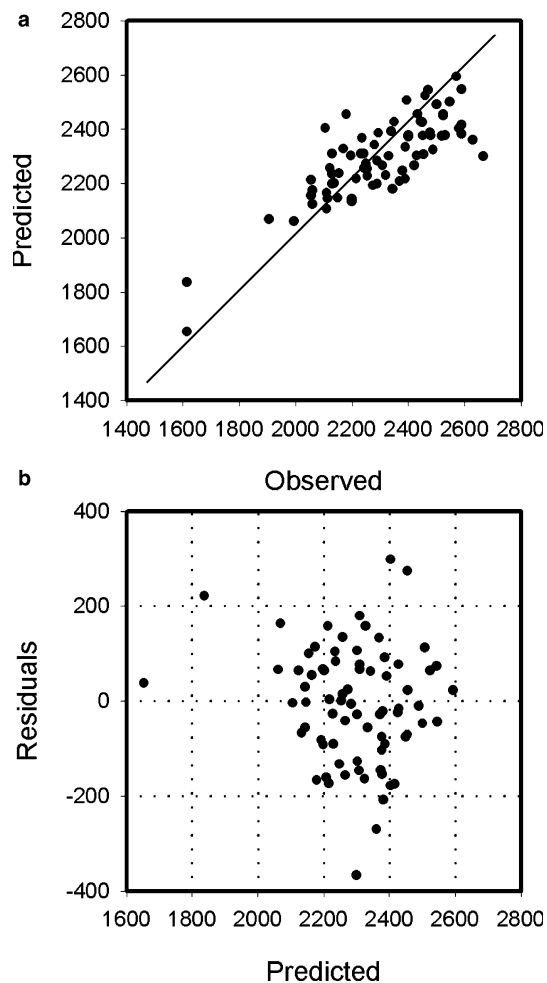


Fig. 5 Observed versus predicted (leave-one-out method) values of altitude (a) and their residuals (b) obtained using a WA-PLS transfer function based on chrysophytes assemblages from high mountain lakes from the Pyrenees (Table 3)

3.3 Reconstructions of the altitude anomalies in the Pyrenees throughout the Holocene

3.3.1 Core stratigraphy

The sediment core (RCA94) from Lake Redon was a homogeneous dark mud (gyttja) with a few small silt layers containing some small dropstones. At the base there was blue clay, distinctive in colour and hardness, typical of pro-glacial lakes. The nature of the sediment was reflected in the relatively high organic content in the core (Fig. 6), except in the first few centimetres of the core bottom.

The two bottom dates were similar in the last 6 cm of blue clay (Fig. 6). This core section was rejected for further analysis. The sediment top dates were unexpectedly old, and did not agree in absolute values with the ^{210}Pb dating, carried out for the first few centimetres of the core, although the tendency was similar. As we were using bulk sediment, it was assumed that the 920 ^{14}C year BP of the top sample was caused by some old carbon effect. Even in a catchment of granodiorite bedrock, calcite veins or disseminated impurities within the granitoid rock can provide some old carbon (White et al. 1999). Since the waters are very soft, relatively small amounts of old carbon can affect the dating results. Consequently, we decided to subtract the top dating (920 ^{14}C year BP) from all the other dates, assuming that throughout the Holocene the amounts of old carbon in the lake were more or less constant. The errors of the two datings were added and calibration followed Stuiver et al. (1998). Ages and age ranges were obtained from intercepts. When several ages were potentially correct, the one closer to the centre of the age range was selected. The final age-depth model was obtained by simple linear interpolation between dated samples (Fig. 6). In order to validate the dating, we

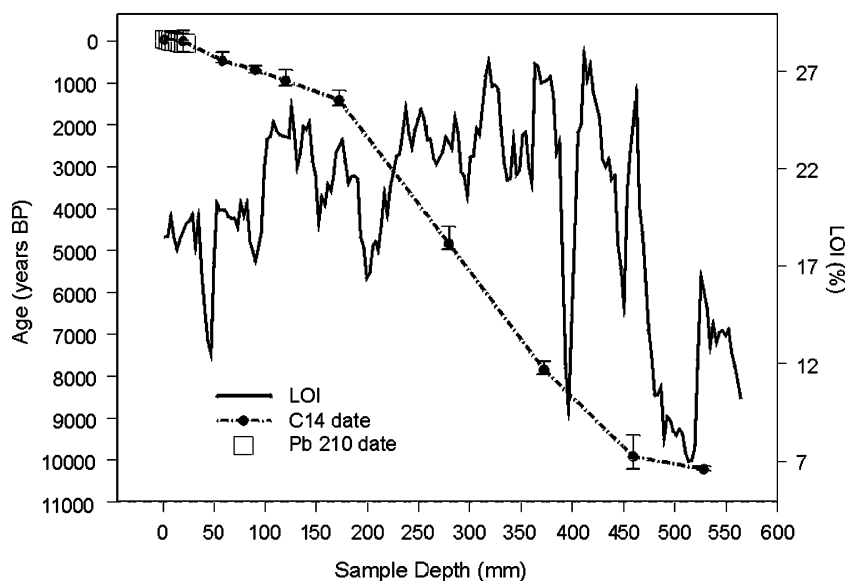
checked the main features of the pollen diagram after applying the age-depth model (Fig. 7a) with previously published pollen diagrams from the Central Pyrenees (Reille and Lowe 1993; Visset et al. 1996), in particular with the pollen diagram from an adjacent site at Bassa d'Hules, Val d'Aran. The agreement supported our study in that at least the main trends of our chronology were correct.

The chrysophyte cyst record obtained showed significant changes throughout the Holocene (Fig. 7b), the most important being ca. 8 kyear BP when S042/S049, the most abundant cyst in the record, increased abruptly and others such as S300, S035 and S342 decreased. A second change was around 5.2 kyear BP, characterised by the expansion of S306, S015, S150, S130 and S319B. Finally, around 1.2 kyear BP started a period, coinciding with a significant change in the sedimentation rate, which was characterised by rapid changes in the species assemblages. During this period there was a decrease of S042/049, increase of S239, S300 and S345, and occurrence of a number of rare cysts, such as S346, S217, S207/341, S243/143 and S111. To a certain extent, the cyst assemblages during this latter period were similar to those previous to 8 kyear BP.

3.3.2 Altitude anomaly reconstruction

The altitude transfer function obtained was applied to the chrysophyte cyst record from Lake Redon (Fig. 8). The main trends in the record had a tendency of decreasing apparent altitude (warming) from 10 to 1.2 kyear BP; followed by an abrupt increase in apparent altitude (cooling) until 700 year BP, when a decreasing tendency started again until the present. Included within these main patterns were significant fluctuations of shorter duration, which were particularly pronounced during the early (>7 kyear BP) and late Holocene

Fig. 6 Age-depth model for the core studied (RCA94) from Lake Redon. *Open squares* indicate the ^{210}Pb dates for the upper samples. Loss of weight on ignition (LOI) is also indicated for each sample throughout the core



(<2 kyear BP), with a stable period in between. The highest value on apparent altitude throughout the Holocene was recorded during a fluctuation at 9 kyear BP (Fig. 8), followed by a steep decrease (warming) until 8.2 kyear BP, when there was a short but very large fluctuation. This latter fluctuation was particularly well recorded in the LOI values (Fig. 6). From 8 to 7 kyear BP, the altitude anomalies were higher than 100 m most of the time, decreasing only at the end of the period.

From 7 to 3 kyear BP the anomaly values ranged from 30 to 130 m above the present level; it was the most stable period during the Holocene. From 3 to 2.1 kyear BP the anomalies were lower than in the previous period, similar to present values or slightly lower. Then, from 2.1 to 1.6 kyear BP the altitude anomalies returned to the values from mid-Holocene. Considering the Holocene period, if the main trends and extreme events were removed, an underlying pattern of cycles of about 2,000 years seems to be present.

For the period 1.6 kyear BP to the present, there was a higher resolution in the record, because of a higher sedimentation rate. From 1.6 to 1 kyear BP the anomalies were the lowest within the whole record. Then, the altitude anomalies increased by about 200 m. From 980 to 780 kyear BP the values were similar to those from early Holocene. From then to the present, the altitude anomalies decreased, but with significant oscillations of about 250 year cycles, with periods towards lower altitude anomalies at 750–650, 560–450 and 200–100 years BP and periods towards higher anomalies at 650–550, 450–350, 180 and 100–25 years BP.

3.3.3 Climatic interpretation of the altitude anomaly

If we consider the present lapse rate in the Pyrenees (Agustí-Panareda and Thompson 2002), the ca. 250 m range of reconstructed altitude anomalies implied fluctuations in a range of ca. 1.5°C in mean annual temperature, which is in the range expected within the Holocene (Broecker 2001). Chrysophytes are photosynthetic algae and, therefore, they grow during the ice-free period. However, it has been shown that the chrysophytes assemblages in mountain lakes are mainly related to the timing of the ice-cover melting or the length of the ice-cover period, rather than to any climatic component during the summer season (Pla 1999; Kamenik 2001; Kamenik et al. 2001). This is because the phytoplankton growth after ice melting, and of the chrysophytes as a main component of phytoplankton in those lakes, is influenced by the amount of nutrient release in deep sediments during winter (the higher the longer the winter season), the length of the water column mixing during spring overturn (the longer the earlier the cover thaw), and the development of the stratification (the faster the later the ice cover thaw) (Catalan 2000). In addition, the nature of this early productive event conditioned the nature of the successional sequence of the species throughout the ice-free period (Felip et al. 1999). As a

consequence, it is more probable that the reconstructed anomalies using chrysophyte cysts reflected the winter and spring conditions rather than summer or autumn climate conditions.

The modern analogues of the pollen record indicated a higher continentality in the first part of the Holocene than in the second (Fig. 9). All modern analogues pointed to warmer summers associated with continentality; however, for winter temperatures, warmer and colder temperatures than in late Holocene were possible. According to the modern analogues, low winter temperatures were particularly probable before 7 kyear BP, which is in agreement with the chrysophyte record. Therefore, we suggest that the altitude anomaly reconstructed using the chrysophyte cyst has to be interpreted as a winter/spring climate signal.

3.3.4 Comparison with other climatic records

For the last 1,500 years our record presented a larger variability than during most of the Holocene. The apparently larger fluctuations in the most recent millennia could be simply due to the increase in resolution of the record, which consisted of time slices of about 100 years throughout most of the Holocene, whereas they were of ca. 30 years for the most recent period. The higher the resolution, the lower the degree of the signal smoothing. Therefore, we will comment separately on the two distinct parts of the record.

In Fig. 10, we show a conversion of the altitude anomaly to winter mean temperature for the last 1,500 years using the present lapse rate (5.235°C/1,000 m) for the cold months of the year (Agustí-Panareda and Thompson 2002), with the aim to facilitate comparisons with instrumental or documentary records. The Warm Medieval period (WMP) starting at ca. AD 900 was the warmest period in our record. However, by AD 1,000 there was a steep decrease of about 1°C in 100 years, being the period between AD 1,050 and 1,175 within the coldest winters in historical times. This is in agreement with documentary winter temperature reconstructions showing that for the period between AD 1,090 and 1,179 winter temperatures within the WMP were at the level of the Little Ice Age (LIA) (Pfister et al. 1998). The earliest very cold winter in our record (AD 1,050) could correspond to the Great Winter of AD 1,076/1,077, which affected all of western Europe, including northeastern Spain (Pfister et al. 1998). The thirteenth century was again warmer, with a temperature drop again early in the fourteenth century. The cold period around AD 1,350 in our record agrees with the very cold winters AD 1,352–1,355 recorded in the GISP2 ice core (Stuiver et al. 1995), the low temperatures reconstructed for the Northern Hemisphere (Mann 2003) and the estimated low radiation (Bard et al. 2000). The winters were warmer again during the late fourteenth and mid-fifteenth centuries, and decreased again for the late fifteenth and early sixteenth century. From early in the

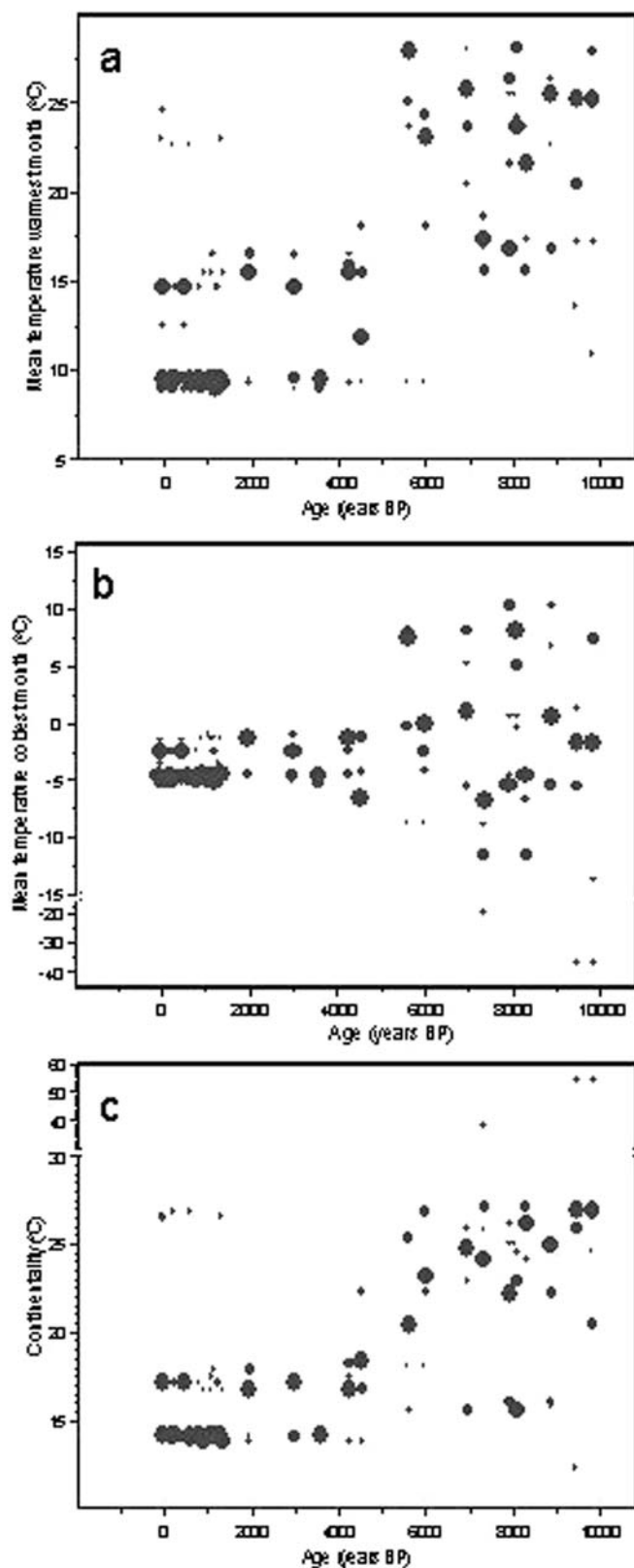


Fig. 9 Temperature of the warmest (a) and coldest (b) months and continentality (c) of sites with the four closer modern pollen analogues for the RCA94 pollen record (Lake Redon, Pyrenees). The larger the size of the symbol the closer the modern analogue to the fossil sample

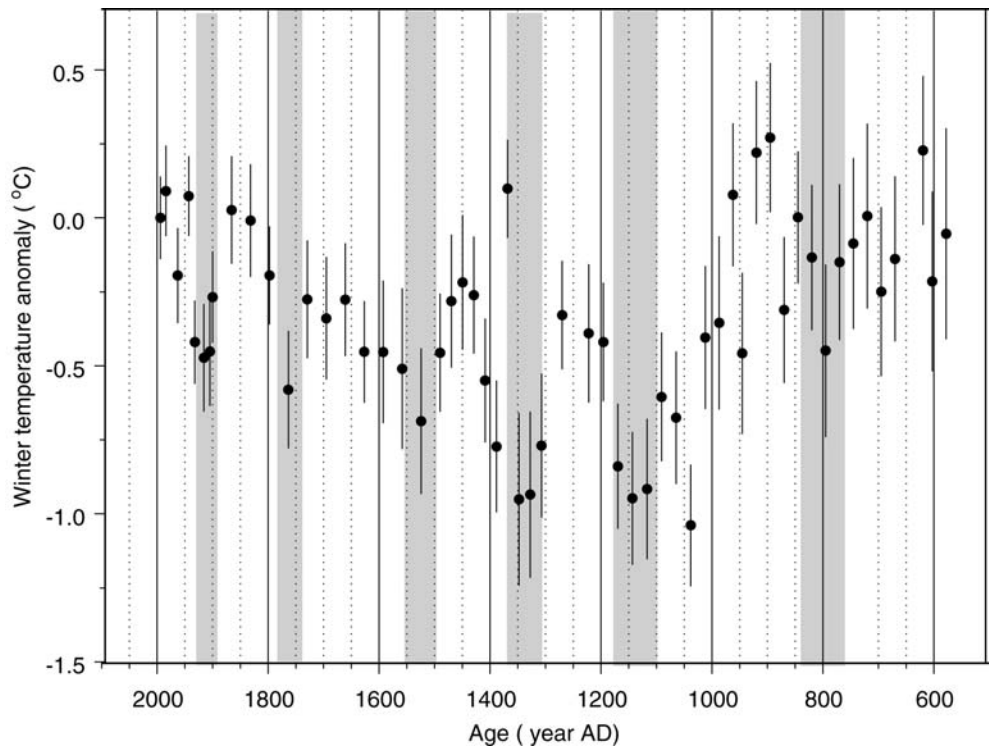
sixteenth century to the present, there was a warming trend with cold oscillations in the late eighteenth century and the early twentieth century. The inferred temperatures in our record for the cold periods since the sixteenth century were warmer than for previous LIA cold phases, which is without agreement with the reconstructed mean annual temperatures in the Northern Hemisphere (Mann 2003). This disagreement could reflect regional winter particularities or could be a consequence of the methodological uncertainties. The resolution in our record is rather low for this period, and so we cannot discard saying that the intensity of cold period of duration of a few decades is smoothed or completely hidden, particularly if interannual variability within those periods was high.

The last cold oscillation recorded corresponded to the 1962/1963 winter. This has been the last outstanding winter, very cold and with heavy snowfalls, from the Pyrenees up to Barcelona. The blocking high-pressure system with its centre close to the Iceland area led to persistent easterly and northerly flows over extensive parts of the continental Europe. The cold air advection followed after pronounced cyclonic activity connected with remarkable amounts of snow in the northwestern Mediterranean. This winter has been proposed as an analogue for the Great Winter 1076/1077 (Pfister et al. 1998). To some extent this situation could be considered as an analogue for the cold winter period during the second part of the WMP.

Considering the whole Holocene, our reconstruction showed a warming trend until 4 kyear BP (Fig. 8). This trend does not agree with the general tendency shown by other proxies with a higher influence of the warm period of the year such as pollen (Reille and Lowe 1993). In those records, there is a climatic optimum expanding from early to mid-Holocene, which was also present in the RCA94 pollen record, when reconstructing the warmest month temperature using modern analogues (Fig. 9). Therefore, we suggest that summer and winter tendencies differ throughout the first part of the Holocene, with climate being significantly more continental than after 4 kyear BP. This period coincides with the period of higher monsoon rainfall in Africa, which ended abruptly at mid-Holocene (Gasse 2000; deMenocal 2000).

We subtracted the general warming tendency from our record for comparison of the sub-millennial variability with other records. In Fig. 11, the RCA94 record is compared with the SST reconstruction using the UK37 alkenone index from an Alboran sea core (Cacho et al. 1999). The resolution of the two records was similar for most of the Holocene. Although the marine record shows the summer pattern from continental records, the fluctuations at submillennial scales did agree with RCA94 chrysophyte signal from 10 to 3.5 kyear BP. There was a cooling trend from 10 to 9 kyear BP, which was followed by a steep warming within the period 9–8 kyear BP, within which the 8,200 years BP cold event was embedded according to our record. The two records

Fig. 10 Altitude anomaly reconstruction from RCA94 chrysophyte record converted into winter/spring mean temperatures for the last 1,500 years

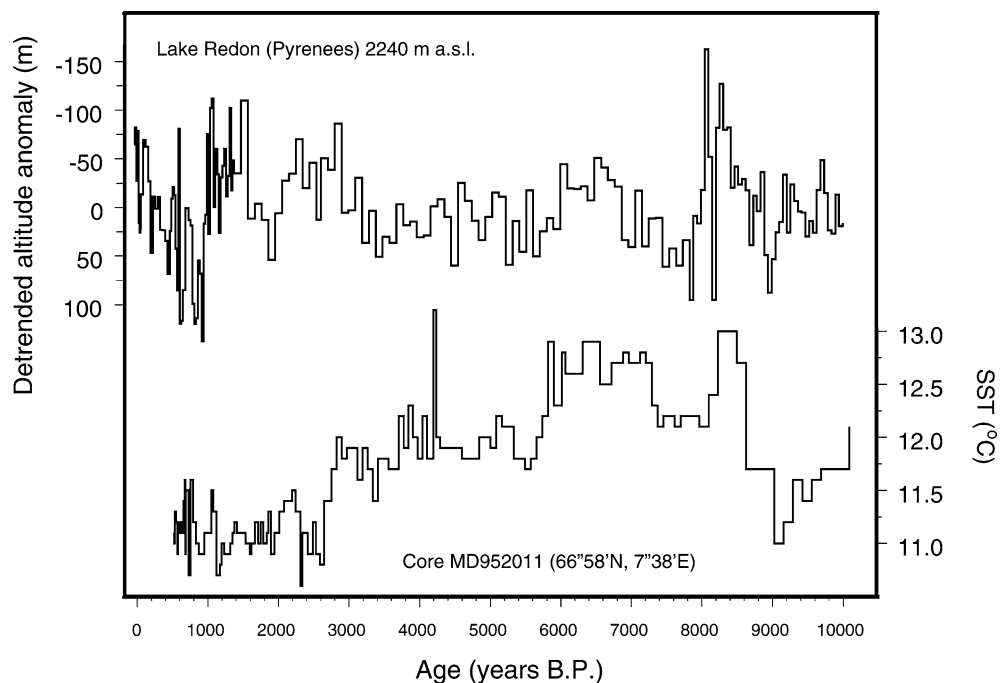


show that the period 6–7 kyear BP was warmer than before (7–8 kyear BP) and after it (6–3.5 kyear BP). The agreement between the two records finishes with the abrupt monsoonal change in Africa.

Although dating uncertainties, the low amplitude of the oscillations and the lower resolution of our record hamper precise comparisons between RCA94 and high resolution records such as GISP2 (Stuiver et al. 1997)

and CC3 (McDermott 2001), some remarkable similarities existed between them (Fig. 12). For the period 1.5–7 kyear BP, RCA94 and CC3 showed a very similar timing in alternative warm (7–5.8, 5–4.6 and 3.1–2 kyear BP) and cold periods (5.7–5.1, 4.5–3.1 and 2–1.5 kyear BP). The latest oscillation corresponded to the so-called Roman warm and dark ages cold periods. Some of the extreme fluctuations during the period 2–7 kyear BP were

Fig. 11 Comparison between the altitude anomaly in the Pyrenees (reconstructed using the chrysophyte record from RCA94) and the SST in the Alboran sea (reconstructed using the UK37 alkenone index (Cacho et al. 1999). The RCA94 have been corrected for the Holocene tendency shown in Fig. 8



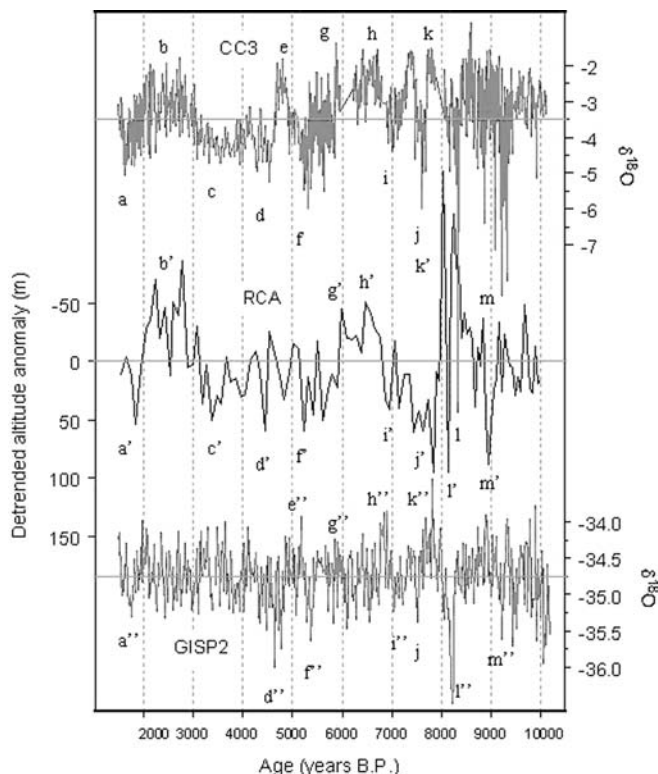


Fig. 12 Comparison of the detrended RCA94 record with $\delta^{18}\text{O}$ data of the CC3 speleothem record in Ireland (McDermott et al. 2001) and the GISP2 ice-core bidecadal record from Greenland (Stuiver et al. 1997)

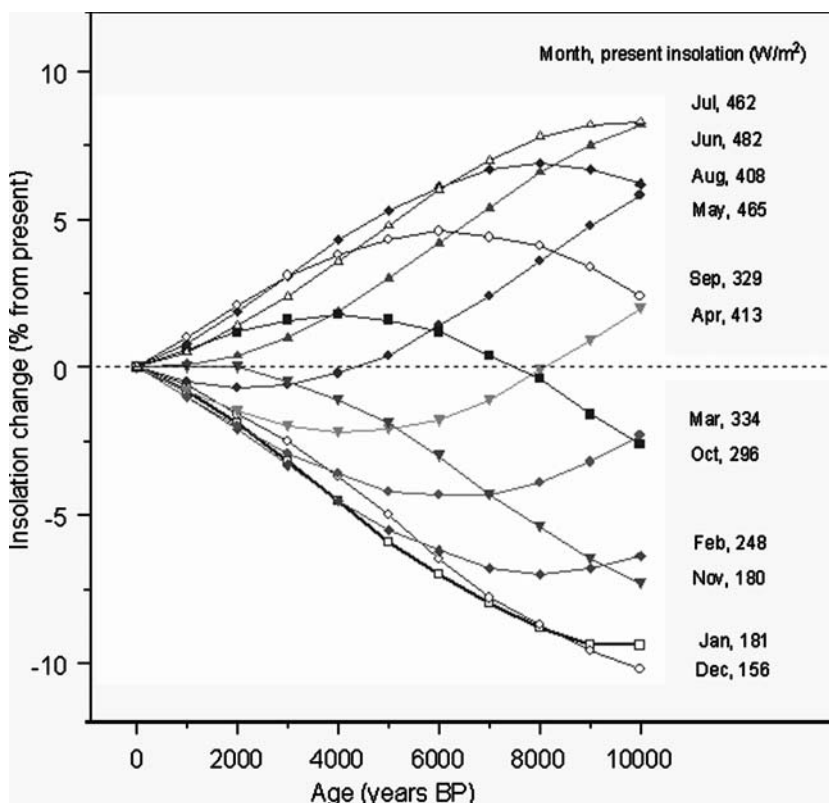
also present in the GISP2 record, as already pointed out in McDermott et al. (2001).

The frequency and intensity of the variations in the early Holocene (>7 kyear BP) were higher than for the most recent period in all three records. The 8,200 year BP event (Alley et al. 1997; Barber et al. 1999) is recognised as the major Holocene $\delta^{18}\text{O}$ event in the GRIP and GISP2 ice cores (Grootes et al. 1993) and it has been found in other Northern Hemisphere records (Klitgaard et al. 1998; Yu and Wright 2001), such as in the CC3 speleothem in SW Ireland (McDermott et al. 2001). The presence of the 8,200 cold event in our record, particularly clear in the LOI signal (Fig. 6), appeared embedded in a warm fluctuation (Fig. 8) according to the cyst signal, but the age of the event matches that in the GISP2 record. In the RCA94, the warm fluctuation was followed by a cold phase that lasted for most of the 7–8 kyear BP millennium. The CC3 record also shows warm fluctuations before and after the 8,200 event, although the trough of the cold fluctuation is broader than in the RCA94 record. Within the 7–8 kyear BP millennium, CC3 also shows a cold fluctuation. Finally, the three records agree in a number of cold events between 8.8 and 9.2 kyear BP, prior to the 8.2 cold event.

3.4 Concluding remarks

The altitudinal variation of the chrysophyte cysts assemblages in high mountain lakes appears related to

Fig. 13 Change in monthly insolation throughout the Holocene at latitude 40°N (Berger 1978)



winter/spring climate components that determine the length of the ice cover (Pla 1999; Kamenik 2001). Therefore, the use of the chrysophyte cyst records for climate reconstructions may provide a valuable complement to other proxies that are more influenced by the conditions during the warm season; such is the case of terrestrial vegetation. However, specific calibration will be required for each lake district where the method would be applied as the relationship between altitude and climatic conditions will depend on the latitude and other features of the lake district (e.g. bedrock substrate) or mountain range location. Conversion to mean winter/spring temperatures can be intended using present lapse rates. Although there is no guarantee that those lapse rates were constant throughout long time periods, it is reasonable to assume that they were similar within historical times, as used in this study, or perhaps even during the Holocene. In that sense, the temperature accuracy in our reconstructions is within the lowest part of the range obtained until the present for continental aquatic flora and fauna remains (Lotter et al. 1997; Walker et al. 1997; Rosén et al. 2000; Larocque et al. 2001; Bigler and Hall 2002; Bloom et al. 2003; Heiri et al. 2003). Further progress in the understanding of the chrysophyte ecology may provide a more precise climatic interpretation of the observed altitudinal cline in the distribution of the chrysophyte cysts.

Accepting that the altitude anomaly reconstructed represents winter/spring climate, it is apparent from the RCA94 record that in the northwestern Mediterranean there was a winter warming during the early Holocene, which represented a progressive reduction in the continentality of the climate, particularly when mid-Holocene summer temperatures decreased substantially as indicated by the RCA94 pollen record. This trend is consistent with the orbital monthly insolation changes occurring throughout the Holocene at this latitude (Fig. 13).

The variations of the RCA94 detrended altitude anomaly showed a higher similarity to the SST reconstructions from Alboran Sea for the early and mid-Holocene and to the North Atlantic record of the CC3 speleothems from 7 kyear BP to the present. The higher correlation of the RCA94 record with the North Atlantic variability in the most recent periods might be due to a decreasing effect of the monsoon influence in the area, which could be associated with the higher continentality of the early and mid-Holocene climate conditions. All in all, the extreme variations in early Holocene were also recorded in RCA94. We suggest that the lack of a broader recording of the 8,200 cold event in the Mediterranean could be due to its overlapping with a warm fluctuation in the area, therefore, requiring a higher temporal resolution in the records for showing it, as the event was of short duration. In the lake water level records of Africa, the period ca. 8,200 years BP appears extremely dry (Gasse 2000).

The RCA94 record brings additional evidence of oscillations occurring at about 2,000 years cycles including a warm and cold phase (Bond et al. 1997). However, it also shows that multicentury variability has a detectable impact (McDermott et al. 2001). The chrysophyte cyst record in RCA94 indicates that winters within the MWP could be the warmest during the Holocene in the northwestern Mediterranean, with a sudden and steep cooling about 1,000 years ago. If that is correct, before the LIA, there could have been a more continental climate in this area for a few centuries, with some similarity to the early Holocene, warm summers and extremely cold winters. For the last 500 years, the low resolution of our record limits the comparison with recent high-resolution multiproxy reconstructions (Lutgebacher et al. 2004). However, to the extent the comparison is possible, our reconstruction does not show contradictions and agrees in the temperature difference of ca. 0.5°C between the winters of the period AD 1,900–1,500 and those of the twentieth century.

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